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Some structural and floristic aspects of the forest

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Key words. Vegetation type; forest structure; floristic composition; swamp forest; campina; campinarana.

1. Introduction

In flying over the Central Amazonian forest, one would certainly be tempted to describe the landscape as homogeneous if not monotonous. Apart from the water surfaces of the large rivers, it is a uniform, dark green carpet, rippled by innumerable smaller rivers and streams.
However, in penetrating this forest along streams and trails, one observes that, in fact, it represents a mosaic of distinct structural entities. To begin with, there are three main categories of forest: first, forest which is periodically inundated by white water (carrying sediments) of the Amazon River (known as 'várzea'); the second type is forest inundated by the blackwater rivers ('igapó') containing dissolved humic acids as in for example the Rio Negro; the third type of forest is that of the so-called 'terra-firme', i.e. upland, which is not subject to periodic inundations by the big river systems.
To prevent misunderstanding, it must be stressed that this study concerns only the last category of forests. We use specifically the term forest on terra-firme as defined by Prance[22] for the forest of a well-drained plateau and of slopes descending towards stream beds ('baixios').
Following the few studies already made on the natural vegetation of the terra-firme, as opposed to igapó and várzea, and according to several years of our own observations, four major forest types may be distinguished: terra-firme forest in the restricted sense; 'campina'; 'campinarana'; and swamp forest. Although these four forest types are functionally related, each exhibits its own structural and functional characteristics, which, for purely methodological reasons, will be presented separately. (The term 'structure' has been used in different ways[29]. Here it refers to the spatial organization, the second characteristic of an ecosystem is its functioning, that is, its organization in time[32].) Only structural characteristics, including floristic data, are presented here, and some aspects of interrelations will be considered at the end. Up to the present, human activity has had little impact; the forest landscape is essentially intact with the exception of small strips along the few roads and larger rivers with their secondary forests, and more or less cultivated areas in the immediate proximity of recent settlements. Secondary forests, the so-called 'capoeira', are excluded from this study.

2. Vegetation types

2.1. The forest on terra-firme

2.1.1. General organization. For the intact terra-firme forests of hydrographic basins such as the area we have studied at Reserve – km 60, which includes plateaux and slopes, it is possible to distinguish four vertical layers: trees above 15 m in height; trees from 12–15 m; small trees and shrubs from 7–12 m; and lower shrubs and saplings from ground level to 7 m.
Considering similar topographic sites, the top layer is remarkably homogeneous in appearance and includes two superposed structural 'sets of trees of the present' (in other words, 'trees that lack any potential for further expansion'), and one 'set of trees of the future' (or, trees that 'still have a potential for future expansion'[20]). This 'set of the future' may be absent in certain areas.
The second layer is variable in structure yet represents always one 'set of the present' or a 'set of the future', the foliage of which constitutes a neat and important trophic unit. The third and fourth layers are essentially homogeneous in their spatial pattern, but show a tendency towards simplification on the slopes in that the third layer is markedly more complex on the plateau.
These four layers result from the spatial distribution of erect and rigid plants such as trees, shrubs, palms, saplings as well as the ground herbs, which constitute the 'synusiae' of the mechanically independent autotrophs (a synusia being a group of plants 'of similar life-form, filling the same niche and playing a similar role, in the community of which it forms a part'[27]), and which present the skeleton for the synusiae of the mechanically dependent plants such as lianas, stranglers, epiphytes and heterotrophs, which distribute themselves according to their ecological needs and to the habitats available. We consider here only vascular plants. Little research has been done on non-vascular plants, bryophytes, lichens, algae and fungi, even though they are very common. Apart

from the fundamental activity of fungi in the degradation and assimilation processes of the organic matter, we may emphasize the particular importance of the bryophytes and lichens as ecological indicators of microclimatic conditions.

2.1.2. Trees and shrubs. Heights. The highest trees of the region, exceeding 35 m, are the following:
Diniza excelsa (Mimosaceae) 44–39 m
Hevea guianensis (Euphorbiaceae) 43.5–36.3
Callophylum angulare (Guttifereae) 40.5
Goupia glabra (Celastraceae) 40.5–37.5
Minquartia guianensis (Olacaceae) 40
Nectandra rubra (Lauraceae) 40–37.5–35
Tabebuia incana (Bignoniaceae) 39.3–35.5
Cedrelinga catenaeformis (Mimosaceae) 39
Cariniana micrantha (Lecythidaceae) 39–37–36.9
Peltogyne paniculata (Caesalpiniaceae) 37.5
Copaifera multijuga (Caesalpiniaceae) 37.5
Osteophloeum platyspermum (Myristicaceae) 36.5
(After Alencar et al.[2] and Prance et al.[25].)
Diniza excelsa is certainly the tallest tree of the Amazonian forest. Ducke[11] cited a height of 55 m for a felled tree.
The frequency of emergent trees which exceed 30 m is low, for instance 4/ha[25], 2/1600 m^2[30] and 3/1800 m^2 (3 × 600 m^2)[15], but increases with the altitude above sea level of the respective plateaux (as determined from aerial photographs). Meter-by-meter measurements accomplished by Prance et al.[25] in their admirably complete inventory show two frequency peaks for trees of 15 m and 6 m in height. These two peaks correspond to the second and fourth layers defined above. The trees of 14–16 m in height represent, approximately, one quarter of all individuals per ha (120/492). In the Ducke Forest Reserve, Aubréville[6] listed 147 individuals of 1–7 m, 17 of 7–15 m, and 17 exceeding 15 m, in 500 m^2; for 175 m^2 the numbers were 65, 11 and 9 respectively, and furthermore, he counted 1194 stalks of less than 1 m.

Diameters. The measured diameters are low, as are those of heights. The only trees which reached values above 85 cm were:
Diniza excelsa (Mimosaceae) 200 m^{+}
Osteophloeum platyspermum (Myristicaceae) 155^{++}
Unidentified 155^{++}
Cedrelinga catenaeformis (Mimosaceae) 150–91^{+++}
Lecythis paraensis (Lecythidaceae) 115^{++}
Nectandra rubra (Lauraceae) 96^{+}
Holopyxidium sp. (Lecythidaceae) 91^{++}
Peltogyne catingae subsp. *glabra* (Caesalpiniaceae) 90^{+++}
Cariniana micrantha (Lecythidaceae) 89–87^{+++}
Caryocar pallidum (Caryocaraceae) 88^{++++}
(After $^{+}$ Guillaumet and Kahn[15], $^{++}$ Takeuchi[30], $^{+++}$ Alencar et al.[2], $^{++++}$ Prance et al.[25].)
In the inventory of R. Onety, analyzed by Aubréville[6], the largest diameters were attributed to: *Diniza excelsa* (Mimosaceae), *Caryocar* sp. (Caryocaraceae), *Manilkara* sp. (Sapotaceae) and *Cedrelinga catenaeformis* (Mimosaceae).
Rodriguez[28] cites some more trees with diameters larger than 85 cm, namely: *Scleronema micranthum* (Bombaceae), *Ocotea rubra* (Lauraceae), *Minquartia guianensis* (Olacaceae), *Aldina heterophylla* (Caesalpiniaceae), *Qualea paraensis* (Vochysiaceae), *Dipterix odorata* (Papilionaceae), *Brosimum potabile* (Moraceae) and *Swartzia reticulata* (Caesalpiniaceae).
Assuming an exponential distribution of size classes (from DBA 5 cm upwards) the category of smallest trees is, nevertheless, still over-represented, and this is still true for trees with DBA above 15 cm. As shown in table 1, the variation of tree numbers between plots is considerable. Unfortunately, the methods used by various authors to document tree frequencies and distributions are so discordant that their results cannot be presented under a unified scheme. This regrettable state of affairs, however, may itself be the result of the very complexity of forest structure. The values for the basal area (sum of tree cross-sections) calculated by different authors for trees with diameters exceeding 15 cm and referring to 1 ha are 28, 36 and 25 m^2 [15,16].

Table 1. Numbers of trees in various localities

No. plots	Size of plots	Range of No. trees per plot	Ref.
Diameters > 5 cm			
1	400 m^2	56	25
2	800 m^2	102–129	25
4	600 m^2	91–100–107–116	15
Diameters > 8 cm			
1	10000 m^2	745	17
Diameters > 15 cm			
10	800 m^2	17–17–20–23–29–29–32–35–36–37	25
Diameters > 16 cm			
1	1600 m^2	104	25
1	400 m^2	31	25

Buttresses and stilt roots. These root formations are certainly one of the most notable characteristics of tropical forests, and they are not uncommon. Among one hundred nearest-neighbor trees with diameters of 15 cm and above, observed in the Ducke Forest Reserve, 19 had buttresses and 2 had stilt roots (Annonaceae). The buttresses did not exceed a height of 1 m, with the exception of those of two unidentified trees which reached 2.5 and 4.5 m. Among the species with buttresses are those cited by Takeuchi[30]: *Couepia elata* (Chrysobalanaceae), *Brosimum* sp. (Moraceae), *Lucuma* sp. (Sapotaceae), *Vantanea* sp. (Humiriaceae), *Protium* sp. (Burseraceae), *Sclerolobium* sp. (Caesalpiniaceae), *Eschweilera* sp. (Lecythidaceae) and one unidentified Leguminoseae.

The palms. A detailed description of palm distribution is presented and discussed by F. Kahn in this review. Nevertheless, some general features should be mentioned in this survey of general forest composition.
The palms present perhaps the most characteristic physiognomical element of the terra-firme forest north of Manaus, both with regard to number and the area they occupy. Seedings below 1 m are abundant everywhere and acaulous species such as *Astrocaryum* aff. *javarense* and *Attalea attaleoides* constitute a neat layer of 1.8–2.5 m with their long, divided leaves. The smaller uni- or multiple-stemmed species (*Bactris* spp., *Iriartella setigera*, etc.) are abundant, yet occupy little space. Even the tallest species, such as *Oenocarpus bacaba*, as tall as 15 m, do not emerge through the canopy. Of a total of 84

individuals counted within 1660 m^2, only a single *Scheelea* sp. and two *Oenocarpus bacaba* were taller than 15 m^{25}.

The few data available before F. Kahn's inventories were made are not strictly comparable but reflect, nevertheless, the abundance and diversity of the group:

1 ha: 16 individuals (3 sp.), diameter above 8 cm[17]; 1600 m^2: 112 ind. (4 sp.), complete inventory[30]; 500 m^2: 82 ind. (11 sp.), above 1 m in height[6]; 175 m^2: 109 ind. (13 sp.), complete inventory[6]; 1 ha: 8 ind. (2 sp.), diameter above 15 cm[25]; 12 × 600 m^2: mean of 60 ind. (36–78), above 1 m in height[15]; 7200 m^2: 2326 ind., complete inventory (1350 above 1 m in height)[16].

Floristic composition. In a forest at km 30 of the Manaus – Itacoatiara road, Prance et al.[25] listed 179 tree species with stem diameters (DBH) larger than 15 cm in 1 ha and 56 species with 5–14.9 cm in a plot of 400 × 400 m within this hectare. The total of 235 species listed in table 2 belong to 43 families.

Table 2. Tree families of the forest on terra-firme[25]

	Sp.	Gen.
7 families comprising more than 10 species		
Lecythidaceae	18	4
Moraceae	15	10
Sapotaceae	14	9
Burseraceae	12	2
Caesalpiniaceae	12	5
Annonaceae	11	6
Chrysobalanaceae	11	4
10 families with 5–9 species		
Mimosaceae	9	4
Lauraceae	8	4
Vochysiaceae	8	3
Melastomaceae	8	2
Rubiaceae	7	7
Myrtaceae	7	4
Apocynaceae	6	5
Violaceae	6	4
Meliaceae	6	2
Myristicaceae	5	2
14 families with 2–4 species		
Euphorbiaceae	4	4
Flacourtiaceae	4	2
Papilionaceae	4	3
Elaeocarpaceae	3	1
Humiriaceae	3	2
Olacaceae	3	3
Palmaceae	3	2
Sapindaceae	3	2
Sterculiaceae	3	2
Bombacaceae	2	2
Dichapetalaceae	2	1
Hippocrateaceae	2	1
Monimiaceae	2	1
Nyctaginaceae	2	1
12 families with 1 species		
Caryocaraceae		
Celastraceae		
Combretaceae		
Connaraceae		
Duckeodendraceae		
Guttifereae		
Ochnaceae		
Opiliaceae		
Quiinaceae		
Rhamnaceae		
Simarubaceae		
Tiliaceae		

Perhaps not surprisingly, in view of this extreme diversity, individual species are poorly represented. Thus 11 species, comprising 82 individuals, make up 25.43% of all trees with DBH > 15 cm. The most frequent species is *Eschweilera odora* (Lecythidaceae) with 26 individuals, followed by *Scleronema micranthum* (Bombacaceae) with only 9 individuals per hectare. This example, with is apparently typical for Central Amazonian forests, highlights the difficulties encountered in attempts at natural forest management.

2.1.3. Climbers. Central Amazonian forests appear to be comparatively poor in climbers; the so-called 'matas de cipós' (climber forests) found in other Amazonian regions (for instance in Pará and Rondônia), do not occur. This is not to say that the climbers are of low abundance, but unfortunately they are generally not considered in forest inventories, and taxonomic identification remains difficult. Systematic counts carried out together with F. Kahn in three plots of 20 m × 30 m (600 m^2), four different transects in each, resulted in table 3. Note that this inventory does not include the small herbaceous climbers which are found on practically every tree.

Table 3. Number of climbers in 600 m^2 with stem DBH 5 cm along transects in the INPA Forest Reserve km 60

Toposequence	Plateau	Crest	Slope
1	16	10	16
2	6	7	18
3	7	4	0
4	8	6	6

In the Ducke Forest Reserve, in a plot of 175 m^2, Aubréville[6] listed 131 lianas less than 1 m long, and 22 longer than 1 m; in another plot of 500 m^2 he found 44 individuals longer than 1 m.

These climbers belong to diverse families and genera: Leguminoseae, *Acacia multipinnata, Piptadenia multiflora, Mimosa spruceana, Entada polyphylla, Derris* spp., *Bauhinia* spp., etc.; Loganiaceae, *Strychnos* spp.; Apocy-

Table 4. Number of individuals (A) and frequency (B) of the grounds herbs of 50 × 1 m^2 in the Ducke Forest Reserve. (frequency = number of times that a species is recorded within the 50 plots)

	A	B
Hymenophyllaceae		
Trichomanes cf. *hostmannianum*	3	36
T. pinnatum	20	16
Polypodiaceae		
Ctenitis protensa	32	19
Lindsaea lancea	5	3
ind.	2	2
Selaginellaceae		
Selaginella parkeri	2	2
S. sp.	2	1
Gramineae		
ind.	20	10
Marantaceae		
ind.	7	6
Heliconiaceae		
Heliconia sp.	3	3
Cyperaceae		
Hypolytrum laxum	4	3
Rubiaceae		
Geophila cordifolia	1	1
Psychotria?	1	1
Melastomataceae		
ind.	2	2

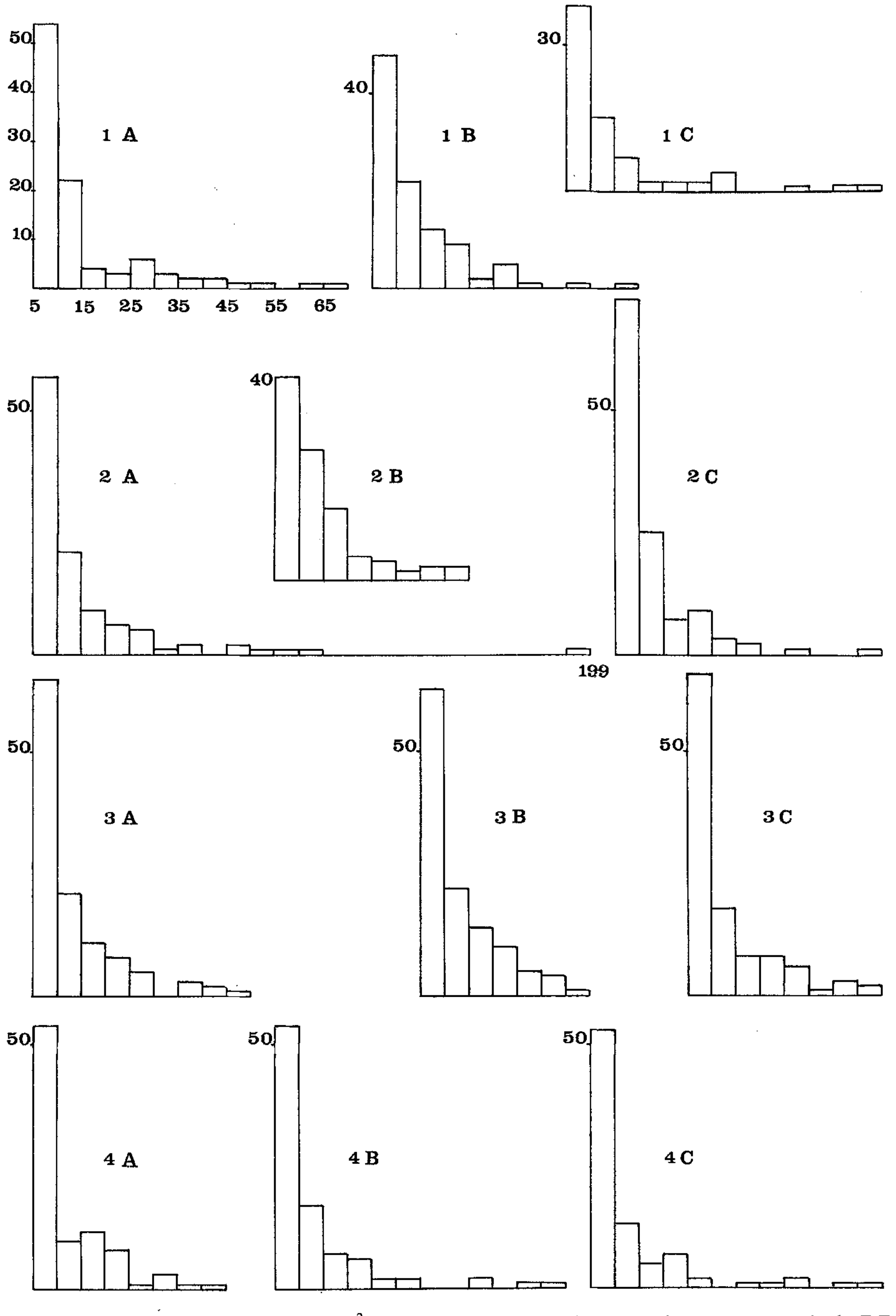


Figure 1. Forest on terra-firme: diameter class in 3 plots of 600 m^2 (A = plateau; B = crest; C = slop) of 4 toposequences in the E.E.T.S. of the INPA[15].

naceae, various genera and species of Landolphiae; Dilleniaceae, *Davilla* spp., *Dolicocarpus* spp.; Menispermaceae; Bignoniaceae, etc.

In contrast to Asian and African forests, climbing palms are represented only by a single genus, *Desmoncus*, which although it comprises several species, never reaches significant frequencies. The following herbaceous climbers are still less frequent: *Dioscorea* (Dioscoreaceae), *Smilax* (Smilacaceae) and various species of Piperaceae, Asclepiadaceae, Menispermaceae, etc.

2.1.4. Stranglers, epiphytes and semi-parasites. With the exception of the semi-parasites, these categories are difficult to define as they include various intermediate forms; furthermore, they are represented by numerous taxons, usually with high frequencies.

The climbers which climb trees with their adhesive roots may completely give up their attachment to the soil and develop into true epiphytes or else they may remain linked with the soil by long aerial roots (semi-epiphytes or pseudo-epiphytes). To these belong diverse species of the fam. Araceae, specifically of the genera *Philodendron, Heteropsis, Anthurium*, etc., of the Cyclanthaceae, Marcgraviaceae, Piperaceae *(Peperomia)*, Gesneriaceae *(Codonanthe)*, Polypodiaceae *(Lomariopsis)*, Melastomataceae, etc., and the two very remarkable Hymeno-

phyllaceae *(Trichomanes ankersii* and *T.* aff. *pedicellatum)* with their small fronds practically glued to the base of the trunks and climbing up to 50–60 cm.
The Central Amazonian forest is particularly rich in these types of plants, both in terms of species and individuals. Even on small trees diverse species, represented by several individuals in different developmental stages, are quite commonly found.
The stranglers are represented by the Moraceae *(Ficus)* and Clusiaceae (*Clusia, Havetiopsis,* etc.). They are very abundant but do not by any means always strangle their host trees. Almost all larger trees harbor one or several individuals in a more or less advanced stage of development. The most abundant epiphytes in terms of species and individuals belong to the Pteridophytes, Bromeliaceae and Orchidaceae and to a lesser extent to the Araceae, Araliaceae, Cactaceae, Gesneriaceae, Piperaceae. Quantitative data on these plant categories is, however, difficult to find. To the best of our knowledge the only estimate available is that of Takeuchi[30]: 19 individual epiphytes in 600 m^2 of forest on the plateau. This seems a rather low value and, being an isolated sample, is not representative. On a single tree we counted 5 species of Orchidaceae, 5 of Bromeliaceae, 2 Clusiaceae and 1 Cactaceae, amounting to 30 to 40 individuals. A single species of Orchidaceae *(Maxillaria)* was represented by 9 individuals or groups of individuals and of Bromeliaceae *(Aechmea)* by 8 young plants.

The very frequent representatives of about a dozen genera of the Loranthaceae are usually invisible from the ground due to their position within the foliage of the canopy.

2.1.5. Ground herbs. As is generally the case for the moist, evergreen forests of the tropics, the forests of Central Amazonia have a poorly developed herbaceous layer. For instance, a sampling series of 50 × 1 m^2 in the Ducke Forest Reserve resulted in a mean of 2 developed herbs/m^2 with a maximum of 9 herbs/m^2 and included 10 m^2 which were devoid of herbaceous growth. Fourteen species with individuals in all developmental stages were listed (Table 4). These data do not include an average of 4 seedlings of unidentified woody plants per m^2, nor the mean of 3.4 species of developed woody plants per m^2. The distribution of herbaceous species seems to be related to light intensity as is the case for the fern *Ctenitis protensa,* as well as to soil conditions. The selaginellas, for example, are particularly frequent on abandoned termite colonies. The conditions for those herbaceous plants favor asexual reproduction by such means as stolons, epiphyllous buds, etc.; a mode of growth that leads by necessity to patchy distribution of small, single-species colonies. The acaulous *Cycadales, Zamia* cf. *obidensis,* which occur sporadically in groups of 2–3, merit special mention.

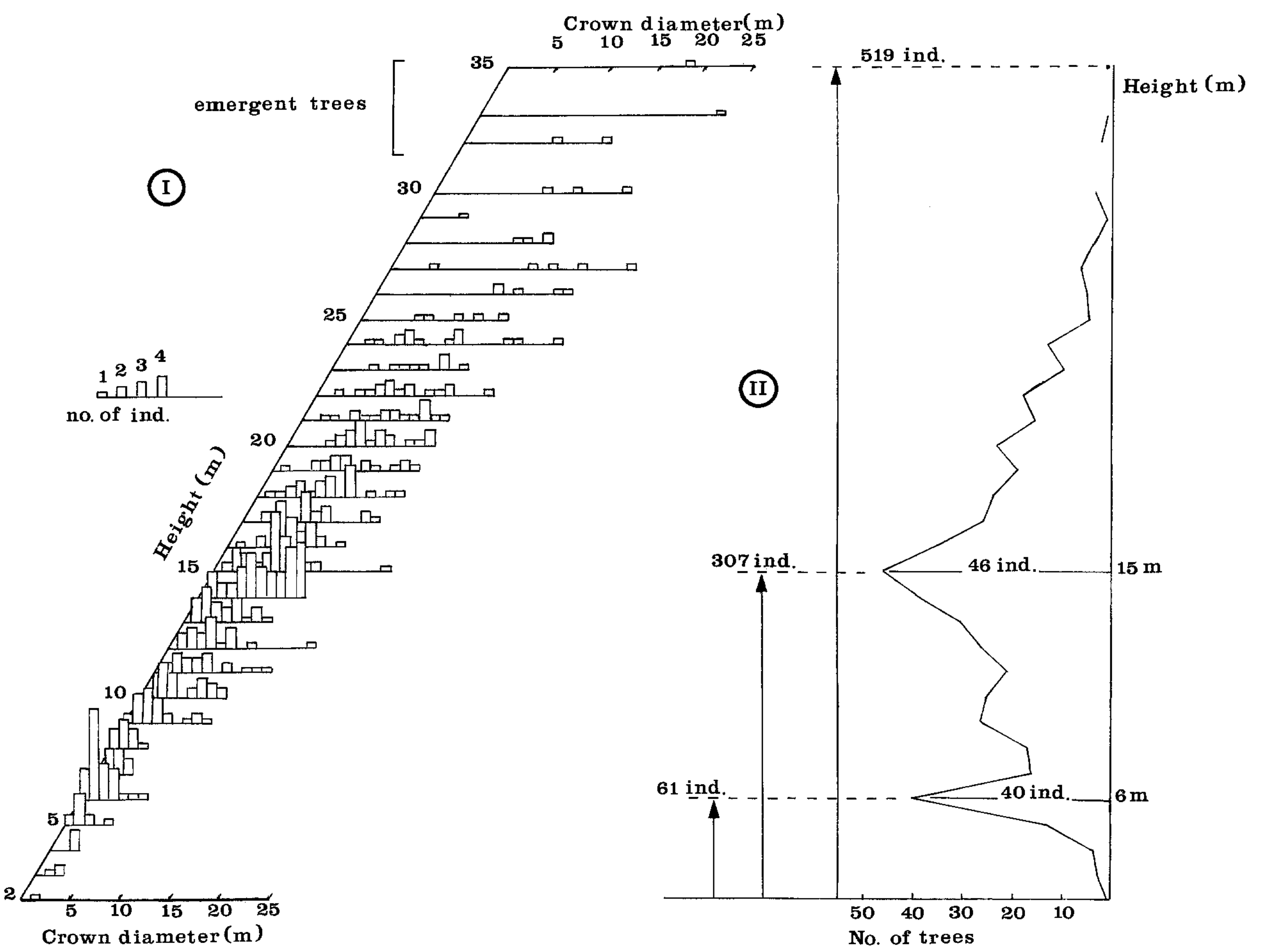


Figure 2. Forest on terra-firme: I. number of shrubs and trees and crown diameters in relation to height. II. Total for height[25].

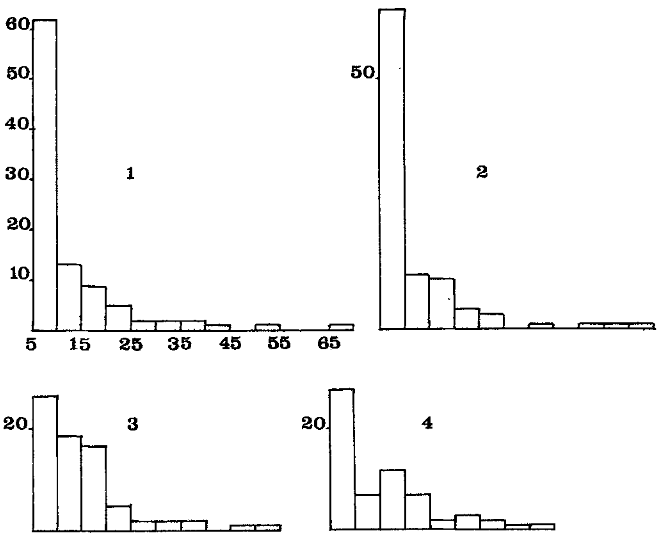


Figure 3. Swamp forest: diameter class in 4 plots of 600 m^2 in the E.E.T.S. of the INPA[15].

2.1.6. The saprophytes. Although of generally inconspicuous habitus, the saprophytes are, nevertheless, remarkable for their species richness and for their specific modifications: Triuridaceae *(Sciaphila purpurea* and *S. albescens)*, Burmanniaceae *(* g. *Apteria, Campylosiphon, Dictyostegia, Gymnosiphon)* and Gentianaceae *(Voyria* and *Lephaimos)*.

In contrast to the relatively dull-colored flowers of the Monocotyledons, those of the Gentianaceae are often a luminous yellow, white, or lilac. The root system of *Lephaimos spruceana* is reduced to the finest rhizoids fixed on the lower surface of dead leaves, whereas *Sciaphyla purpurea* penetrates to a depth of ±25 cm and in one specimen of *Voyria* sp. we gave up the search for the root tips when digging reached a depth of 60 cm.

The leafless habit and the subterraneous mode of growth with different flowering seasons render proper sampling practically impossible. Nevertheless, on twelve plots of 100 m^2 we counted four individuals of a single species of the Burmanniaceae and two individuals of the genus *Lephaimos* (Gentianaceae).

2.2. Swamp forest

The forest of the hydromorphic soils of the stream valley bottoms, very poorly, known so far, does not exceed a height of 30 m. Referring to vertical structure, one observes an upper arborescent stratum (layer) (from 12–14 to 25–30 m) in which of crowns of the higher palms intermingle with the canopy of the larger trees. The palm species *(Mauritia flexuosa, M. aculeata, Jessenia bataua, Iriartea exorrhiza, Euterpe precatoria)* increase in number per area as the width of the valley and the water content of the soil increase. Below, the space is essentially occupied by tree and palm trunks overgrown by root-climbing lianas and epiphytes, by younger palms, by trees and by shrubs. Finally, in the lowest 5 m we find a very dense vegetation of acaulous or pseudo-acaulous palms *(Manicaria saccifera, Attalea* aff. *spectabilis, Astrocaryum acaule)*, of young palms, of large Monocotyledons, of some rather infrequent species of large Dicotyledons and of saplings. Monocotyledons and ferns are especially frequent. The basal area appears to be lower than in the forest of the plateau. The only measurements obtainable up to date are presented in figure 3. According to the data of Takeuchi[30] *Scleronema micranthum* (Bombacaceae) is the highest tree, and also has the largest trunk diameter (123 cm); *Vitex sprucei* (Verbenaceae) reaches 90 cm in diameter and *Chromolucama rubriflora* (Sapotaceae) barely 80 cm. Buttresses are common; *Pourouma myrmecophylla* (Moraceae), *Pouteria cyrtobotrya* (Sapotaceae), *Xylopia amazonica* (Annonaceae), *Protium* spp. (Burseraceae), etc., as well as stilt roots; Annonaceae sp., *Pouruma* spp. (Moraceae) and pneumatophores, *Symphonia globulifera* (Guttifereae), *Mauritia flexuosa, Euterpe* sp., *Iriartea exorrhiza* (Palmae).

The inventory of Porto et al.[21] includes 95 Dicotyledenous tree species distributed in 33 families.

Only four species make up 30% of the total number of individuals: *Carapa procera* (Meliaceae), *Vitex sprucei* (Verbenaceae), *Euterpe precatoria* and *Jessenia bataua* (Palmaceae); and with seven additional species contribute already more than 50% of the population: *Chromolucuma rubriflora* (Sapotaceae), *Eschweilera odora* (Lecythidaceae), *Mabea caudata* (Euphorbiaceae), *Xylopia amazonica* (Annonaceae), *Licania micrantha* (Chrysobalanaceae), *Iryanthera macrophylla* and *I. elliptica* (Myristicaceae). Strangely enough, with the exception of *Euterpe precatoria* and *Jessenia bataua*, the palms are weakly represented in this particular sample series. This is undoubtedly due to the heterogeneity of this forest, as emphasized by the authors. The two species cited above appeared in 9 of 10 samples, yet *Mauritia flexuosa*, occupying the third place in abundance, was present in only 3/10 samples with 8 individuals. Our own counts[15] on four smaller plots (600 m^2) show 68, 92, 114 and 119 palms (exceeding 1 m in hight). Takeuchi[29] list 176 palms on 2200 m^2 without, however, specifying their size category; the number of seedlings was 118 in a single m^2 assessed.

Other Monocotyledons, such as Marantaceae, Zingiberaceae, Costaceae, Rapateaceae, Cyclanthaceae, Strelitziaceae, Heliconiaceae are often abundant in patches of single-species stands. The family Thurniaceae, with a single species, is only found in the swamp forest and prefers stream banks. In addition there are several Cyperaceae and Bromeliaceae which are specific to poorly drained soils.

In general, Monocotyledons are much in evidence in these swamp forest and, although no concrete numbers are yet available for Central Amazonia, it appears probable that Lindemann's figures from Surinam, cited by de Granville[13], apply equally to this region, namely the Monocotyledons account for 12 to 31% of the species of the flowering plants.

2.3. The 'campina'

The word 'campina' was introduced into botanical language by A. Ducke in 1922[11]. He explained this word as the diminutive of the Portuguese 'campo' = field. Nevertheless, 'ka'apĩ' exists in a tupi language[14] and refers to a dry and low little forest (P. Grenand, pers. com.). The bibliography related to campina and campinara is abundant. In addition to the references cited here the reader is

Table 5. Tree families of the swamp forest[21]

	Sp.	Gen.		Sp.	Gen.
6 families comprising more than 5 species					
Euphorbiaceae	8	6	Sapotaceae	8	5
Lauraceae	8	3 (or 4)	Annonaceae	7	4
Myristicaceae	8	3	Meliaceae	6	3
Guttifereae	5	3	Chrysobalanaceae	2	2
Moraceae	4	3	Dichapetalaceae	2	1
Apocynaceae	3	2	Elaeocarpaceae	2	1
Bombacaceae	3	2	Humiriaceae	2	1
Burseraceae	3	1	Olacaceae	2	2
Lecythidaceae	3	2			

16 families with 1 species		
Anacardiaceae	Myrsinaceae	Sterculiaceae
Borraginaceae	Ochnaceae	Tiliaceae
Combretaceae	Peridiscaceae	Verbenaceae
Flacourtiaceae	Rubiaceae	Violaceae
Lacistemataceae	Sabiaceae	
Monimiaceae	Simarubaceae	

referred to 'Estudos sobre a vegetação das campinas', Acta amazon. *5* (1975), *6* (1976).

The mere existence of this extraordinary vegetation attracted the interests of naturalists long ago. In the drab uniformity of the vast expanse of tall evergreen forests, the campinas, with their open sand 'clumps' of bushes and small trees, are a welcome and unexpected experience. Rooted in poor podzols they allow for high intensities of light to penetrate and show a marked tendency towards xeromorphy. The trees are tortuous and many-branched. Vascular epiphytes, lichens, mosses and liverworts are abundant on trees as well as on the ground.

One may distinguish several facies which Anderson[3] considers as natural plant communities, these include:

– white open sands partly colonized by blue algae *(Stigonema tomentosum* and *S. panniforme)* and by dense tufts of *Eriocaulon* sp. (Eriocaulaceae);

Table 6. Floristic comparison of a campina and campinarana[5]

	Campinarana		Campina	
	Sp.	Gen.	Sp.	Gen.
Anacardiaceae	1	1	–	–
Annonaceae	3	3	1	1
Apocynaceae	2	2	1	1
Bombacaceae	1	1	–	–
Burseraceae	2	2	1	1
Caesalpiniaceae	2	2	1	1
Chrysobalanaceae	3	3	1	1
Erythroxylaceae	1	1	1	1
Euphorbiaceae	3	3	–	–
Guttifereae	3	1	1	1
Humiriaceae	–	–	1	1
Lauraceae	3	3	–	–
Lecythidaceae	1	1	–	–
Melastomataceae	2	2	3	3
Meliaceae	1	1	–	–
Mimosaceae	1	1	–	–
Moraceae	1	1	–	–
Myristicaceae	2	2	–	–
Myrsinaceae	1	1	1	1
Myrtaceae	2	2	3	2
Ochnaceae	1	1	1	1
Olacaceae	1	1	–	–
Palmaceae	4	4	–	–
Papilionaceae	3	3	2	2
Rubiaceae	4	4	3	3
Sapindaceae	3	2	2	2
Sapotaceae	4	3	2	2
Simarubaceae	1	1	–	–
Vochysiaceae	1	1	–	–

– islands of vegetation which increase their species richness with size, fringed by lichen *Cladonia* spp. and, going towards the interior other species of lichens as well as Bryophytes; eventually, towards the center, Pteridophytes *(Schizaea incurvata)*, Gramineae *(Axonopus flabelliformis)* and orchids *(Epidendrum huebneri, Encyclia tarumana)* appear;

– thickets of *Ouratea spruceana* (Ochnaceae), *Pagamea duckei* (Rubiaceae) and various Melastomataceae, with a gradual transition to a moderately diversified low and open forest with three prevalent species: *Glycoxylon inophyllum* (Sapotaceae), *Adina heterophylla* (Caesalpiniaceae) and *Pagamea duckei* (Rubiaceae). The understory is still very open and harbors a great abundance of mosses, liverworts and ground herbs, specifically Bromeliaceae and Orchidaceae. Epiphytes are abundant; trees may be loaded with Orchidaceae, Bromeliaceae, Araceae, Ericaceae, Pteridophytes, Bryophytes and lichens.

This is not the place to enter into a discussion on the terminology of the campina biotopes; interested readers will find a good review by Braga[10].

For our purpose we retain only the two categories made for convenience by Anderson et al.[5] based on two characteristics; size of islands and percent of total vegetative cover. Hence an island size below 1 m^2 and total cover 50% is referred to as a 'campina aberta', whereas higher values are referred to as 'campina sombreada'. Clearly, between extreme values one finds all transitional stages.

The flora of the campina is poor. In the campina of the E.E.S.T. of INPA, the only campina analyzed to data[5], one finds less than 40 species of lignous plants, distributed among 15 families. Anderson[3] lists 55 vascular ground plants for the campina and campinarana (table 6) together. The ground plants, epiphytes and non-vascular plants are, one the other hand, especially abundant: 17 genera and 31 species or Orchidaceae[9], and 34 Bryophytes with 5 families of mosses and 7 of liverworts[18].

2.4. *The 'campinarana'*

The popular term 'campinarana' takes its origin from the tupi language: 'rana' = pseudo, hence 'pseudo-campina', also referred to as 'campina alta'. The campinarana is, in fact, neither a campina nor a true, dense forest, but a low, relatively light forest with thin-stemmed trees 10–20 m high with the exceptional large, broad-trunked individual, with or without buttresses. The understory is patchy, that is, in places it is well developed, whereas the herbaceous layer is all but absent. Table 6 compares the floristic compositions of the campina and the campinarana, and table 7 shows, using the example of the two important families, Bromeliaceae and Orchidaceae, that both formations have endemic species. On the whole the campinaranas are more frequent than the campinas, but very

Table 7. Comparison between the families Bromeliaceae and Orchidaceae in campina and campinarana[3]

	Bromeliaceae		Orchidaceae	
	Total	Exclusive species	Total	Exclusive species
Campina	4	0	17	4
Campinarana	7	3	31	18
Campina and campinarana	4		13	

little comparative and quantitative data on their extension and specific flora is known to date.

3. General considerations

3.1. Vegetation types

Although the popular Brazilian language enables the naming of the various types of vegetation with accuracy it is, nevertheless, necessary to identify their proper position within scientific terminology (table 8).

The terra-firme forest (in this restricted sense) is essentially evergreen: of 47 tree species with known phenology, 29 are evergreen, 16 semi-deciduous (losing most, but not all, of their foliage periodically) and 6 are fully deciduous[2,7]. This isolated sample agrees with the general observations of an evergreen canopy the year round but with periods of increased litter fall as shown by Luizão[19].

The characterization of the campinas and campinaranas is more difficult as a consequence of the free use of the terms and of the various floristic entities assigned to them. The campinarana as defined by Braga[10] is, typically, an edaphic form of the tropical rain forest associated with sandy podzols. The campina, whatever aspect is taken, whether structural, edaphic or floristic, is divided between *evergreen mainly sclerophyllous woodland* ('... trees at least 5 m tall with crowns not usually touching but with a coverage of at least 40%. A herbaceous synusia may be present') and *scrubs* ('mainly composed of caespitose woody phanerophytes 0.5 to 5 m tall')[30].

3.2. Floristic comparisons

Although differences in sampling, particularly with regard to plot size and tree diameter, do not allow for strictly quantitative comparisons, it is nevertheless possible to contrast the more general aspects of the woody plant populations in the four different forests reviewed above; the terra-firme forest (in the restricted sense, see above), swamp forest, campina and campinarana.

Perhaps the most striking observation is the following: *not one single tree species occurs in all four forest types*. Only three species are known to be common to three of the formations, that is to the terra-firme forest, the swamp forest and the campinarana; these are *Scleronoma micranthum* (Bombacaceae), *Eperua bijuga* (Caesalpiniaceae) and *Minquartia guianensis* (Olacaceae).

The more complex similarities are shown in figures 4 and 5. The floristic relationships of the campinas and campinaranas are indicated in figure 6 in which all vascular ground plants listed by Anderson[3] are considered.

The currently available information regarding these four forest types which is reviewed here indicates that they are

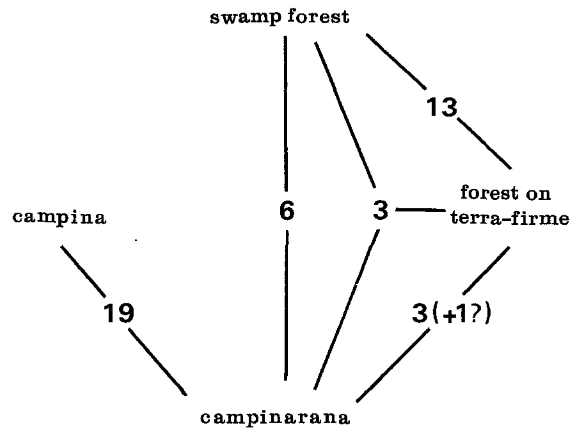


Figure 4. Numbers of lignous plants common to the vegetal formation.

profoundly different; this fact provides an enormous scientific challenge and poses distinct problems with relation to conservation and economic planning of land use. In addition, it is important to remember at this stage that this review does not include the inundation forests nor capoeira, that is, the secondary forest types.

3.3. Vegetation, soil and relief

The basic determinants of the four forest types are of an edaphic character. Each of them is associated with well-defined and specific soils, namely: forest on terra-firme: clayey latsols; campinarana: sandy latosols; campina: podzols; swamp forest: hydromorphic soils;

The recent work of Boulet, Chauvel and Lucas (Convênio CNPq/INPA/ORSTOM[8], see also the article by A. Chauvel in this issue) shows that these soils have their origin in a single basic geological material: the continental sediments of the so-called 'Barreira formation', and that the evolution of the relief is due to geochemical processes. Hence, there is an intimate relation between soil, relief and vegetation.

The plateaux are uniformly covered by latosols and their associated terra-firme forests. The stream valley bottoms are hydromorphic in various degrees and harbor the swamp forests.

There is a continuous evolution between the headwater regions, which are still essentially characterized by latosols and terra-firme forest, and the somewhat less inclined middle courses of the streams with differentiated podzols. It is in this latter region that the campinas establish themselves. The campinaranas cover the transition zone. It is remarkable that, while there is a continuous transition between soil characteristics, there is no con-

Table 8. Comparison of the terms used for the types of vegetation

Usual terms	Projeto Radambrasil[26]	G. T. Prance[22]	UNESCO classification[31]
Mata de terra-firme (forest on terra-firme) Campinarana	– ombrophilous closed low land forest – woody closed campinarana	Forest on terra-firme – high forest with large biomass – campina forest on sandy	Tropical ombrophilous low land forest (conventionally: tropical rain forest). 1. IA. 1a.
Campinas – aberta (open) – sombreada (shallowed)	Campinarana – graminoid – lignous – lignous open	Campina (low vegetation on white sand) of lower Rio Negro	Evergreen mainly sclerophyllous scrubs and woodland. IIA–IIIA1.
Floresta de baixio ou de pântanos (Swamp forest)	Swamp forest	Swamp forest	Tropical ombrophilous swamp forest, dominated by palms. 15. I. lg. (2)

	f.t.f.	s.f.	c.rana	camp.
forest on terra-firme		7,4	2,7	0
swamp forest	3,9		6,9	0
campinarana	1,8	3,6		32,2
campina	0	0	27,8	

Sørensen's index

Jacquard's index

Figure 5. Application of the similarity coefficients of Jaccard and Sørensen. The primary index gives greater weight to the species that are unique in either formation; the second to the species that recur in the two formations (see text).

tinuous transition between the three forest types. These discontinuities are poorly understood.

The fact that sandy podzols are the last state in an extended pedomorphic process, and not, as formerly assumed, direct fluvial deposits, leads to the necessary conclusion that the vegetation of the campinas is neither a community of pioneer plants[12] nor a type of secondary forest resulting from deforestation in historical times, although there seems to be little doubt that the campinas were preferred for settlement by Indian populations[4, 23, 24]. The blue algae *(Stigonema)* and the *Eriocaulon* sp. should, therefore, be seen as the ultimate stage in the evolution of the plant community that parallels the evolution of the soil.

3.4. Variation within forest types

Apart from the physical and chemical properties of soils which are the prime cause of the basic floristic variations, two further major factors should be considered: the relief (i.e. topographic conditions) and silvigenetic cycles.

The forest of the terra-firme covers essentially the plateaux and the slopes. Kahn[16] argues convincingly that 'seule la forêt du plateau présente une architecture pleinement réalisée ... (et que) ... le modèle est bien un facteur

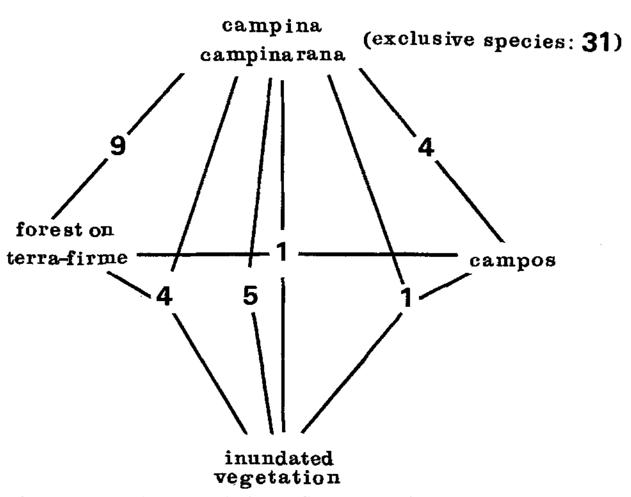


Figure 6. Vascular ground plants: floristic relations of the campinas and campinaranas with forest on terra-firme, campos and inundated vegetation[3].

Table 9. Importance of the relief, soil and sylvigenetic cycle in the vegetal formations

	Relief	Soil	Sylvigenetic cycle
Forest on terra-firme	+ +	+	+ + +
Swamp forest	–	+ + +	+ +
Campinarana	–	+ + +	+ +
Campina	–	+ + +	–

de variation de l'architecture forestière ... (bien que) ... l'effet de pente (soit) masqué par la variabilité imposée par le cycle silvigénétique' (... only on the plateau is the potential forest fully realized [and that] ... the relief is a natural factor of variation in forest architecture [although] the effect of the slope is masked by variations imposed by the silvigenetic cycles).

The internal regeneration of the vegetation, based on the mechanism of tree falls and reconstitution, manifesting itself by the juxtaposition of patches in various phases of floristic and structural development, is particularly important in the terra-firme forest. In the swamp forest the degree of hydromorphy is the overriding determinant of the pattern of variation; in the very open campinas, integral regeneration cycles have practically no effect on overall architecture and even in the campinarana their effects are relatively slight.

The relative weight of the various factors influencing variation in the four forest types is depicted in table 9.

4. Conclusion

In this review, the prime objective has been to attempt a succinct analysis of the forest landscape in the region of Manaus, and to demonstrate that the apparent homogeneity of the vast forest expanse is, in reality, a mosaic resulting from the continuous dynamism of the physical environment, of pedogenesis and of regenerative processes.

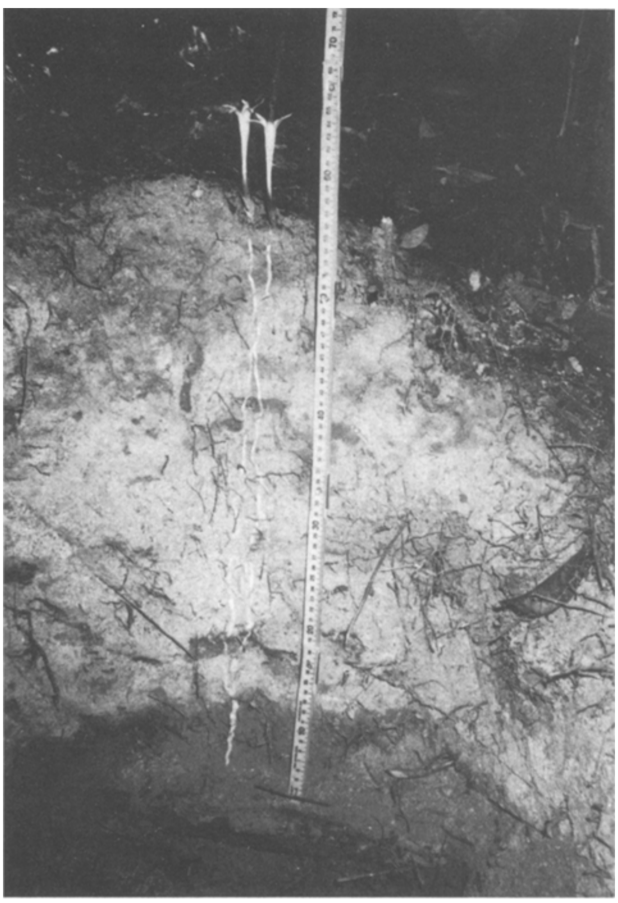
Rather than consolidating our knowledge, it therefore widens our view on all the problems requiring further study. The terra-firme forest needs, perhaps, the most intensive efforts, since it is the most complex of the forest types and also occupies by far the largest portion of land. It has been, and still is, the most exploited forest and it will, without doubt, be subject to the most intensive transformations in the future. Precise knowledge of its internal function is a precondition for non-destructive land use.

The swamp forests present specific problems for possible agricultural use. Due to their lesser extension and difficult soil conditions they are, for the moment, not the focus of aggressive development schemes.

The campinas and campinaranas are the most fragile formations. Even when a most carefully tended vegetative cover is provided, the return is extremely poor. The most rational solution for man and his environment is to protect them in globo. All four forest types are fragile with regard to man's modern economic aggressivity and thus need the most detailed and careful consideration if irreparable harm and incalculable losses are to be avoided.

Regarding the establishment of biological and ecological reserves, the essentially mosaic composition of the forests ought to be a basic determinant in the delineation of their boundaries.

Habit and simplified spatial arrangement of the trees in a cleared forest.



A saprophyte (g. *Voyria*) and its root system.

Trunks of the swamp forest and epiphytes.

General aspect of campina.

Undergrowth of campinarana.

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The distribution of palms as a function of local topography in Amazonian terra-firme forests

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Key words. Palms; forest architecture; topography; Amazonia.

Introduction

Ten years ago, Moore[8] lamented our ignorance of the ecology of palms, one of the most conspicuous plant families of the Amazonian forest, and he wrote: 'We need to know much more about water, soils, light and temperature relationships ...' Trying to fill in the gap, we initiated a series of ecological investigations on Amazonian palms in 1980 at the National Institute for Amazonian Research (INPA). Some of the results obtained so far will be discussed in this study.

The most general assertion that could be made until now is that palms react to vertical patterns of soil drainage. Bouillenne's[1] description of *Mauritia* formations, Moore's[9] survey of the general features of palm ecology, de Granville's[2] ecological analysis of the monocotyledons of the French Guiana, all agree that the distribution of palm species in lowland forests is related to the presence of hydromorphic or well-drained soils (or more exactly non-hydromorphic soils).

Recently Kahn and Castro[6] tracked the distribution of palms along two catenas (technical term for topographic sequence) at the Experimental Station of Tropical Sylviculture (INPA), near Manaus, in a primary forest, and came to the following conclusions (fig. 1):

– On well-drained soils, the vegetation includes arborescent palms which do not reach the forest canopy; arborescent multiple-stemmed palms do not occur; the palm diversity in the understory (under 10 m in height) is particularly high, up to 17 species per plot of 1200 m^2.

– On poorly-drained soils which are waterlogged during the rainy season, arborescent palms are abundant in the forest canopy, reaching 30 m in height, and arborescent multiple-stemmed palms are frequent; the palm diversity